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FLOW REGULATION, GEOMORPHOLOGY, AND COLORADO RIVER MARSH DEVELOPMENT IN THE GRAND CANYON, ARIZONA[1]

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Abstract. New, productive fluvial marshes may develop along regulated canyon rivers through reduction in flood frequency, thereby increasing diversity, production, and wildlife habitat availability. Few fluvial marshes occurred along the eddy-dominated Colorado River in the Grand Canyon prior to construction of Glen Canyon Dam in 1963. Reduction of flooding after 1963 permitted widespread marsh development. Fluvial marshes exhibited low stability but high resilience, quickly redeveloping after scouring by high flows between 1983 and 1986. In 1991, 253 fluvial wet marshes (cattail/reed and horseweed/Bermudagrass) and 850 dry marshes (horsetail/willow) occupied 25.0 ha (1%) of the 363 km mainstream riparian corridor between Lees Ferry and Diamond Creek, Arizona.

Fluvial marsh development and composition varied in relation to local and reach-based geomorphology, and microsite gradients in inundation frequency and soil texture. Colorado River marsh density (number/km^2) increased with distance downstream, and marshes were larger and more abundant in wide reaches. Wet marsh cattail/reed stands developed on silty loam soils in low velocity depositional environments that were inundated 54% of the days from 1986 to 1991, whereas dry horsetail/willow marshes occupied less frequently inundated sites with sandy soils. Mean marsh standing mass (641 g C/m^2) was comparable with values from regulated alluvial river marshes, but litter retention appeared limited by flow variability in both regulated and unregulated fluvial marshes. We discuss implications of flow management on the four marsh assemblages, and the need for consensus on priorities for management of regulated fluvial wetlands.

Key words: Colorado River; fluvial marshes; geomorphology; Grand Canyon; resilience; river regulation; spatial scale; wetland habitat management.

INTRODUCTION

Fluvial marshes are diverse, productive patches of wetland vegetation that typically occur on hydric soils along streams (Auclair et al. 1976, Cowardin et al. 1979, Mitsch and Gosselink 1993). Most studies of fluvial marshes have taken place in alluvial valleys with meandering streams and floodplains where vegetation is strongly influenced by geomorphic position, flow-related disturbance, and inundation frequency (Auclair et al. 1976, Hupp and Osterkamp 1985, Stromberg and Patten 1991, Stromberg 1993, Auble et al. 1994). Spatial variability in soil moisture, texture, and geochemistry results in wetland vegetation zonation (van der Valk 1981, Kozlowski 1984, Brotherson 1987, Day et al. 1988, Ohmart et al. 1988, Pennings and Callaway 1992). Although many rivers flow, in part, through narrow gorges, studies of temporal and spatial variation in fluvial marsh development and management along large canyon rivers are few.

Fluvial geomorphologists distinguish between geologically constrained rivers and those with unconstrained or alluvial channels (e.g., Mosley 1987). In many canyon rivers, tributary delivery of coarse debris creates channel constrictions and a patchy distribution of fine sediment deposits. Canyon rivers sustain high flood stage velocities and extensive macroturbulence (Baker 1984, Hupp 1988), and deposition of fine-grained sediment typically is restricted to low velocity eddies. This is a distinctly different geomorphic configuration from the typical pattern of floodplains and terraces observed in alluvial rivers (Rubin et al. 1990, Schmidt 1990). Fine-grained eddy deposits are extensive along some canyon rivers, including approxi-

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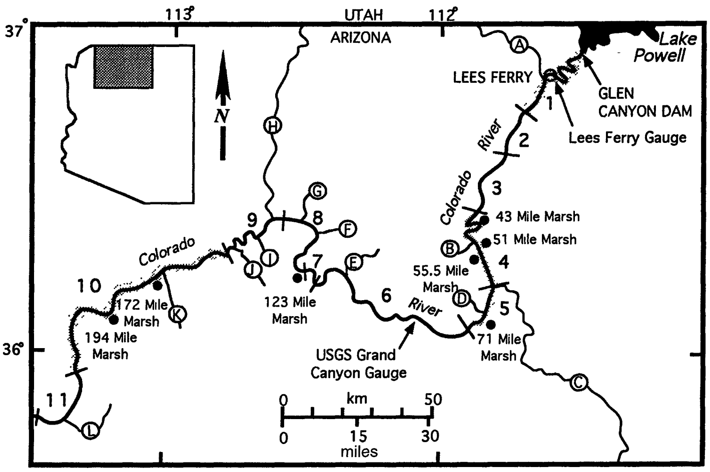

FIG. 1. Location of fluvial marsh study sites in 11 geomorphic reaches (Schmidt and Graf 1990), USGS stream gauging stations, and major tributaries of the Colorado River in Grand Canyon National Park. Reaches include: (1) Permian Reach, (2) Supai Gorge, (3) Redwall Gorge, (4) Marble Canyon, (5) Furnace Flats, (6) Upper Granite Gorge, (7) Aisles, (8) Middle Granite Gorge, (9) Muav Gorge, (10) Lower Canyon Reach, and (11) Lower Granite Gorge. Wide reaches are depicted by wider river lines. Tributaries inventoried for natural fluvial marshes include: (A) Paria R., (B) Nankoweap Cr., (C) Little Colorado R., (D) Chuar Cr., (E) Shinumo Cr., (F) Galloway Cr., (G) Tapeats Cr., (H) Kanab Cr., (I) Matkatamiba Cr., (J) Havasu Cr., (K) Mohawk Cr., (L) Diamond Cr.

mately 200 km (30%) of the Green River in Utah, and the entire 440 km long Grand Canyon of the Colorado River. These conditions are not conducive to wetland or riparian vegetation development and persistence in unregulated rivers (Campbell and Green 1968), as documented in canyon rivers throughout the American Southwest (Clover and Jotter 1944, Turner and Karpiscak 1980, Stephens and Shoemaker 1987, Schmidt and Graf 1990, Webb et al. 1991).

Development of water supplies has led to regulation of many of the world's rivers (Petts 1984, Gore and Petts 1989), and large dams are typically constructed in bedrock canyons. Impoundments destroy upstream riparian habitats (e.g., Woodbury 1959, Ohmart et al. 1988) and often reduce differences between baseflow and flood stage, increase daily flow fluctuations, reduce sediment transport, and alter existing downstream riparian vegetation composition (Baxter 1977, Turner and Karpiscak 1980, Howard and Dolan 1981, Nilsson 1984, Petts 1984, Williams and Wolman 1984, Ohmart et al. 1988, Johnson 1993). Hourly varying discharges produced by hydroelectric power generation create daily "tidal" fluctuations that are accentuated in narrow canyons. Daily tidal, or varial, flows affect riparian soil quality, litter retention and vegetation (Ranwell 1963, Parrondo et al. 1978, Pennings and Callaway 1992).

Wetlands are disappearing at an alarming rate throughout the world, and improved management of water resources and wetland habitats is required to reduce these losses (Risser and Harris 1989). In the United States, wetland area decreased from 159×10^6 ha in the 1780s to 42×10^6 ha in the 1980s (Dahl 1990). Flood control in impounded canyon rivers may lead to development of new, regionally significant riparian vegetation (Turner and Karpiscak 1980, Nilsson 1984, Knopf and Scott 1990, Johnson 1991, Sherrard and Erskine 1991, McDonald and Sidle 1992, Johnson 1993). Management of regulated river vegetation is improving with better predictive capabilities regarding the influence of flow-related factors on wetland assemblages (Harris et al. 1987, Day et al. 1988, Ohmart et al. 1988, Stromberg 1993, Auble et al. 1994); however, the relationship between geomorphology and spatial scale remains unclear in regulated rivers, compromising the effectiveness of management efforts (Risser and Harris 1989).

The Colorado River in the Grand Canyon is one of the most intensively studied, regulated, eddy-dominated rivers in the world. Our studies of marsh development there were motivated by observations of progressive marsh development under flow regulation. In this paper we describe: (1) regulated flow effects on fluvial marsh development; and (2) the distribution, composition, and standing mass of marsh vegetation in 1991 in relation to geomorphology and spatial scale. We discuss the effects of flow regulation on marsh ecology in constrained and eddy-dominated vs. alluvial rivers. Our studies are based on analyses of a large body of serial aerial photographic, hydrologic, and geomorphic data spanning 27 yr of flow regulation, coupled with field observations since 1974. The protection of the Colorado River corridor by virtue of its National Park and World Heritage Site status, make this river system ideal, if not unique, for the study of flow regulation effects on fluvial marsh ecology, and may illuminate management opportunities for fluvial wetlands along regulated rivers.

STUDY AREA

The Colorado River in the Grand Canyon

Our study area includes 363 km of the Colorado River in the Grand Canyon between Lees Ferry (elevation 947 m, 25 km downstream from Glen Canyon Dam) and Diamond Creek, Arizona (404 m elevation, Fig. 1). The Grand Canyon has more than 2400 m of topographic relief. Its climate is continental and arid, with a mean annual precipitation of 215 mm/yr at Phantom Ranch on the Canyon floor (Sellers and Hill 1974). The Colorado River corridor is dominated by riparian deciduous woodland vegetation characteristic of the interior Southwest, with Mohavian interior marshland

and strand assemblages (Brown 1982, Warren et al. 1982). By convention, locations along the river are named as river miles downstream from Lees Ferry, Arizona, and the side of the river is designated as left (L) or right (R), facing downstream. Thus Mile 43L marsh is located at river mile 43, 94 km downstream from Glen Canyon Dam, on the left side of the river (Fig. 1).

Impoundment history

The Colorado River is the largest river in the Southwest and has the highest ratio of reservoir storage to mean annual flow of any large river basin in North America (Hirsch et al. 1990). Glen Canyon Dam impounds Lake Powell reservoir, the second largest reservoir in the United States (Fig. 1). This 200 m high, hypolimnetic release dam was completed in 1963, and has an administratively defined maximum power plant discharge capacity of 892 m^3/s (Water and Power Resources Service 1981). Dam discharges exceed this rate only when the reservoir is full and reservoir inflow rates are high. Glen Canyon Dam reduced the mean pre-dam annual peak flow (2450 m^3/s) by 65%, reduced annual flow variability, increased daily flow variability, and virtually eliminated upriver sediment contributions (Howard and Dolan 1981, Andrews 1991). The mean and annual variability of water temperature was greatly reduced through hypolimnetic release (Minckley 1991), and riparian vegetation colonized the channel margins (Turner and Karpiscak 1980).

The regulated Colorado River has been characterized by "normal flow years" with mean annual flood peaks <892 m^3/s (Fig. 2) and annual flow volumes $<1.22 \times 10^{10}$ m^3. In normal flow years from 1963 to 1991, the range of daily flows sometimes exceeded 790 m^3/s in response to hydroelectric peak power generation, equalling the annual discharge range. Extreme daily discharge fluctuations created "tides" of >3 m. Flows two to three times greater than power plant capacity, and larger annual flow volumes, have occurred during occasional "high flow" years. In high flow years, instantaneous peak discharge at Lees Ferry typically exceeded power plant capacity but daily discharge variability decreased. High releases occurred in 1965 and during 5 yr after Lake Powell filled (1980 and 1983–1986; Fig. 2), but only in 1983 has an annual post-dam flood peak reached mean pre-dam stage.

Geomorphology

Different bedrock formations exposed along the Colorado River cause variation in channel width-to-depth ratio, channel slope, and valley width (Howard and Dolan 1981). These characteristics allowed Schmidt and Graf (1990) to divide the Grand Canyon into 11 geomorphic reaches (Fig. 1). The characteristic channel unit in eddy-dominated rivers is the constriction/expansion/gravel bar complex (Fig. 3B). Channel width is intermittently narrowed by debris fans, rockfall, or landslides, and most of the river's elevational drop occurs in these sections (Leopold 1969). Immediately downstream from constrictions, channel width abruptly increases and large recirculating eddies exist (Schmidt 1990). Downstream from this expansion, the channel narrows slightly and depth decreases over a gravel or cobble bar (Webb et al. 1989, Schmidt et al. 1993).

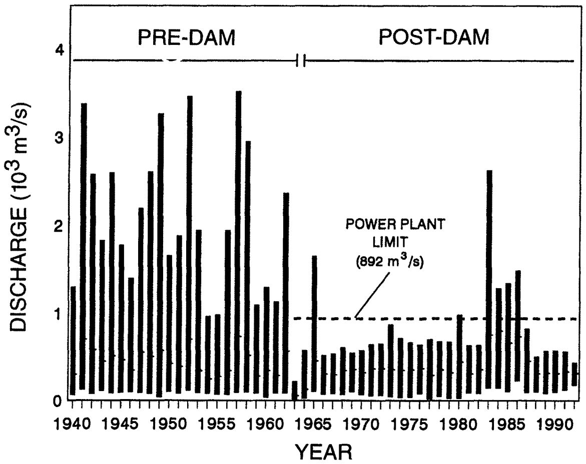

FIG. 2. Time series of annual maximum and minimum daily mean flows of the Colorado River at the U.S. Geological Survey stream gauging station at Lees Ferry, Arizona. The natural hydrograph was characterized by pronounced seasonal spring peak flows with little daily variation. After completion of Glen Canyon Dam in 1963, seasonal variability decreased but daily fluctuations (not shown) associated with hydroelectric power production increased. Flows exceeded power plant capacity (892 m^3/s) in 6 of 29 post-dam yr.

Fine-grained alluvial deposits in eddy-dominated rivers

Fine-grained (<2 mm) alluvial sediment deposits develop at sites where velocity is lowest, particularly in eddies and at channel margins adjacent to wide, low-gradient reaches. Channel constrictions, especially tributary debris fans, control flow separation and thereby control velocity and fine-grained sediment deposition (Schmidt et al. 1993; Fig. 3B). As a result, sand bars and other intermittent patches of fine sediment in eddy-dominated rivers do not migrate as in alluvial river systems.

Fine-grained eddy deposits include separation bars that form near the upstream end of an eddy, reattachment bars that form beneath the primary recirculating eddy cell, and channel-margin deposits distributed along through-flowing reaches (Schmidt 1990; Fig. 3B). The reattachment bar, which is commonly colonized by marsh vegetation, is a sand platform that projects upstream as a spit. The upstream portion of the reattachment bar is separated from the bank by a return current channel (RCC), a scour feature formed by concentrated, recirculating flow when the bar is inundated (Rubin et al. 1990). Many reattachment bar platforms are emergent after flood recession, and the RCC be-

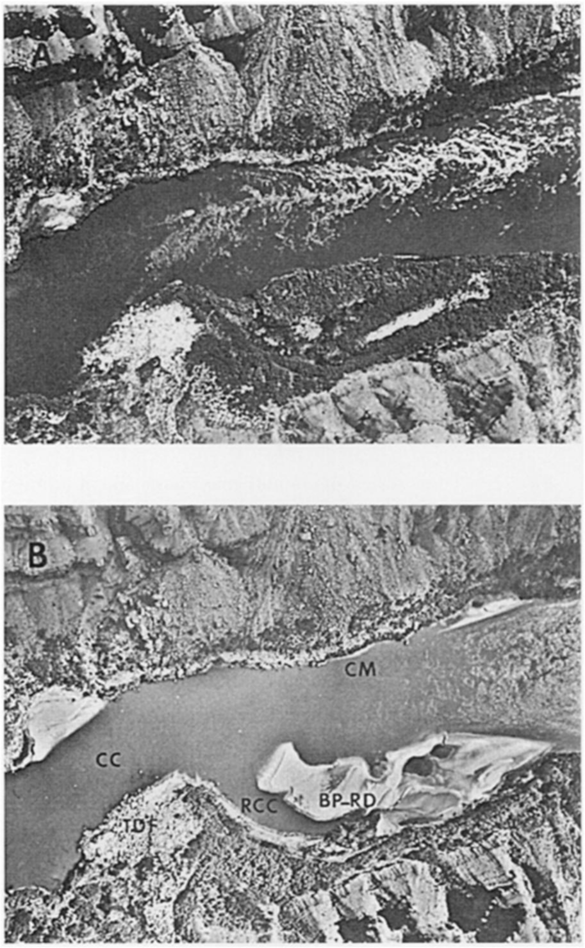

FIG. 3. The geomorphology of the Mile 55.5R eddy and reattachment bar. (A) By 1980 this typical reattachment bar had become completely overgrown by marsh and phreatophyte vegetation. (B) In October 1984 the bar had been scoured of vegetation by 2 yr of high flows, and the geomorphology was visible at a discharge of about 175 m^3/s: BP-RB, bar platform of the reattachment bar; CC, channel constriction formed by the TDF, tributary debris fan, a fixed feature of a small confluent ephemeral drainage that prescribes fine sediment deposition; CM, channel margin environment; RCC, return current channel, a slough-like channel on the shore side of reattachment bars.

comes an area of stagnant flow. Under normal flows, suspended fine sand and silt derived from tributary flows (Randle and Pemberton 1988, Andrews 1991) aggrade in RCCs and are deposited as veneers over coarser mainstream flood deposits (Rubin et al. 1990). RCC deposits contain higher NO_3^- and soluble phosphate concentrations, and have greater water holding capacity than do the sand soils that characterize bar platforms (Stevens and Waring 1988, Stevens and Ayers 1993). The distribution and characteristics of fine-grained deposits are greatly affected by flow regulation and sediment transport (Howard and Dolan 1981, Beus et al. 1985, Schmidt and Graf 1990, Schmidt 1992, Kearsley et al. 1994).

METHODS

Inventories of historic conditions

The distribution of post-dam fluvial marshes through time was evaluated by examining aerial photographs taken in: 1965 (U.S. Geological Survey [USGS], scale 1:15 000, black-and-white), 1973 (USGS, scale 1:7200, black-and-white), 1980 (U.S. Bureau of Reclamation [USBR], scale 1:5000, color-infrared), 1984 (USBR, scale 1:3000, black-and-white) and 1990 (USBR, scale 1:4800, color-infrared). Characteristic patterns of marsh vegetation were determined by comparing Phillips et al. (1977) mapping of marshes with photographic patterns on the 1973 photos, and by comparing field observations with photographic patterns on the 1990 photos. We examined all air photos for these patterns.

Marsh distribution between Lees Ferry and Diamond Creek was comprehensively inventoried in the field during river expeditions in 1982, 1984, 1987, and 1991, with sporadic observations since 1974. We did not record the distribution of horsetail/willow marshes in 1982 or 1987. In 1991 we estimated the size, species composition, and depositional environments of all marshes between Lees Ferry and Diamond Creek.

Field studies of 1991 conditions

Vegetation composition was studied at seven sites considered to be representative reattachment bar marshes in 1991 (Table 1, Fig. 1). Prior conditions were documented at each site with photographic and field inventory data. A series of 1.0 m wide belt transects were established at 10-m intervals across these marshes, perpendicular to local flow direction, with transect length and number, and number of contiguous 1.0-m^2 plots, depending on the size of each marsh. Transect lines were surveyed at 1.0-m^2 intervals in relation to permanent benchmarks for long-term monitoring (Stevens and Ayers 1993).

We measured the basal diameter of all stems of each plant species to the nearest mm at ground level on each 1.0-m^2 plot in each transect. The number and mean diameter of species with exceptionally large stem densities were visually estimated. These measurements provided a direct, nonsacrificial means of monitoring stem density and basal cover of each species for long-term studies. Plant specimens are housed at Northern Arizona University Deaver Herbarium, and taxonomy is based on Phillips et al. (1987) and Welsh et al. (1987).

We related vegetation to soil stratigraphy and texture by excavating three or more 1.0 m deep trenches across each marsh (Stevens and Ayers 1993). Soil samples were dried to constant mass and sieved to determine the size fraction of silt and smaller particles (<0.0625 mm). These data allowed us to evaluate the depositional history of each marsh, and to classify surficial (upper 5 cm) soil texture in each of the belt transect 1.0-m^2 plots.

TABLE 1. Study site locations, characteristics, number of permanent transects and plots, and areal change through time. Sediment deposit types (Schmidt and Graf 1990): RB, reattachment deposit; UP/RB, upper pool deposit in a reattachment deposit depositional environment; RCC, return current channel; BP, bar platform. Standing ash-free dry mass (AFDM, g C/m²) is included. Aerial photography series analyzed include: 1965, 1973, 1980, 1984, and 1990, and field observations from 1975 to 1991.

River mile and side* (distance from Lees Ferry, km)	Deposit type	No. of permanent transects	No. of 1.0-m² plots	n†	1991 standing AFDM (1 SD)	Estimated total marsh area (ha)						
						1965	1973	1980	1984	1987	1990	1991
43L (69)	UP/RB (RCC)	10	51	5	682 (299.7)	0.00	0.00	0.20	0.00	0.00	0.02	0.03
51L (83)	RB (RCC)	10	48		···	0.00	0.00	0.10	0.00	0.00	0.10	0.11
55R (89)	RB (BP)	18	51	5	263 (202.1)	0.00	0.00	···	0.00	0.05	0.49	0.79
71L (114)	RB (BP + RCC)	13	45	4	876 (629.9)	0.00	0.50	0.50	0.01	0.17	0.28	0.35
123L (197)	UP/RB (RCC)	4	19	4	314 (275.5)	0.00	0.01	0.04	0.00	0.00	0.02	0.07
172L (277)	RB (RCC)	9	46	4	906 (822.4)	0.00	0.00	0.03	0.00	0.01	0.19	0.23
194L (312)	RB (RCC)	15	47	6	808 (702.5)	0.00	0.00	0.10	0.00	0.00	0.09	0.26
Total or grand mean	···	79	307	28	642 (579.7)	0.00	0.51	0.87	0.01	0.23	1.19	1.84

* Distance according to Stevens (1983) and measured downstream from Lees Ferry, Arizona. Side of river: L = left, or R = right side looking downstream.

† n = number of 0.5-m² plots on which AFDM was collected.

Total standing mass was determined by collecting all surficial organic matter on four to six additional 0.5-m² plots, randomly located in each study marsh in July 1991. These plots had all been scoured of vegetation by flooding between 1983 and 1986, thus these data represent five years of accumulation of organic matter. Organic matter was dried at 60°C to constant mass and weighed. Subsamples were ashed at 550°C to constant mass and the ratio of organic mass to total mass was used to convert dry standing mass per square metre to ash-free dry mass per square metre.

To compare marsh distribution in regulated vs. unregulated streams, we also measured fluvial marsh size and distribution along 12 large, perennial tributaries (Fig. 1).

Analyses

We employed a weighted frequency method to estimate marsh area from the aerial photographs and field inventories in each geomorphic reach. Marsh patch area was categorized into four ground-truthed size classes: very small (area ≈0.001 ha), small (≈0.01 ha), medium (≈0.1 ha) and large (≈0.5 ha). Because detection of very small marshes from aerial photographs was imprecise, this size class was excluded from the analysis of historical areal change, and we report the distribution of very small marshes only for the 1991 condition. We also excluded fluvial marshes associated with tributary mouths and riverside springs from this historical analysis. Marsh distribution, patch size, and standing mass in 1991 were analyzed using contingency table analysis and analysis of variance (Wilkinson 1990).

We classified marsh vegetation associations using a large, stratified (by elevation), random subsample of the belt transect 1.0-m² plots from the seven study sites (Stevens and Ayers 1993). Fifty-one (where possible) 1.0-m² plots were selected from each study site, and unvegetated plots were subsequently excluded, providing a group of 307 randomly selected 1.0-m² plots (Table 1). We constructed a matrix of the total basal area of each of 76 plant taxa that occurred in these plots. We distinguished four distinct plant associations using TWINSPAN (Hill 1979).

The daily inundation frequency of each 1.0-m² plot was estimated at each site. Stage-to-discharge relations were established at the seven study sites between the 140 and 1150 m³/s stages during a series of U.S. Bureau of Reclamation (1990) discharge tests. Duration curves for daily maximum discharge were developed for water years 1987–1991 for the Lees Ferry (Mile 0) and Grand Canyon (Mile 88) USGS gauging stations (Fig. 1). Daily inundation frequency was related to the stage-to-discharge relationship at each study site on the basis of distance from these gauging stations, and then to each 1.0-m² plot.

The species by plots matrix was ordinated using canonical correspondence analysis (CCA, CANOCO version 2.1, Ter Braak 1992). Rare species were downweighted, and species and plots factor-loading scores were derived from $\log_e + 1$ adjusted total basal area data. Daily inundation frequency, soil texture, interaction between these two variables, and distance downstream were used as environmental predictors for each plot. In addition to univariate analyses of variance, correlations between covarying diversity (species density as the number of species per square metre) and total

TABLE 2. Four marsh plant associations derived from TWINSPAN analysis of n = 307 1.0-m^2 plots in seven marshes, and associated parameters. Numbers following plant names refer to species identified in Fig. 5.

Association	n	Mean inundation frequency (1 SD)	Soil texture	Mean total basal area (cm^2/m^2) (1 SD)	Species richness (S, no./m^2) (1 SD)
1) Clonal wet marsh (cattail/reed) *Typha domingensis* (68), *Phragmites australis* (49), *Juncus torreyana* (40), *J. articulatus* (36), *J. balticus* (37), *J. encifolius* (38), *Carex aquatilis* (17), *Chenopodium* sp. (69), *Equisetum arvense* (28), *Scirpus acutus* (57), *Agrostis stolonifera* (2), *Echinochloa crus-galli* (25), *Veronica anagallis-aquatica* (74)	50	0.54 (0.251)	silty loam	52.9 (80.931)	4.6 (2.914)
2) Nonclonal wet marsh (horseweed/Bermuda-grass) *Conyza canadensis* (22), *Polygonum aviculare* (52), *Cynodon dactylon* (23), *Melilotus alba* and *M. officinale* (43)	43	0.17 (0.17)	loamy sand	14.7 (14.554)	4.9 (2.320)
3) Woody phreatophyte (tamarisk/arrowweed) *Tamarix ramosissima* (65), *Pluchea sericea* (66), *Alhagi camelorum* (3), *Artemisia ludoviciana* (6), *Aster spinosus* (7), *Bromus* spp. (12), *Baccharis salicifolia* (11), *Baccharis sarothroides* (10), *Epilobium adenocaulon* (27), *Erigeron divergens* (31), *Gnaphalium chilense* (33), *Gutierezzia sarothrae* (34), *Hordeum jubatum* (35), *Oenothera hookeri* (46), *O. pallida* (47), *Salix gooddingii* (55), *Salsola iberica* (56), *Sonchus asper* (59), *Sporobolus cryptandrus* (62), *Sporobolus contractus* (61), *Xanthium strumarium* (75), *Castilleja* sp. (16), *Erigonum inflatum* (32), *Centarium calycosum* (18)	68	0.16 (0.197)	sand	39.9 (86.812)	4.5 (2.465)
4) Dry marsh (horsetail/willow) *Equisetum laevigatum* × *hyemale* (29), *Salix exigua* (54), *Andropogon glomeratus* (76), *Artemesia dracunculus* (5), *Aster subulatus* (8), *Baccharis emoryi* (9), *Bromus tectorum* (13), *Bromus wildenowii* (14), *Chrysothamnus nauseosus* (20), *Corispermum nitidum* (21), *Dicoria brandegei* (24), *Elymus canadensis* (26), *Acacia greggii* (1), *Lepidium latifolium* (41), *Muhlenbergia asperifolia* (45), *Plantago lanceolata* (50), *Plantago major* (51), *Polypogon monspeliensis* (53), *Solidago canadensis* (60), *Sporobolus flexuosus* (63), *Taraxacum officinale* (64), *Panicum capillare* (48), *Medicago sativa* (44), *Cercium* sp. (19), *Ambrosia* sp. (4), *Tragopogon dubius* (67), *Mentha arvensis* (42)	146	0.18 (0.194)	sand	16.4 (19.456)	4.7 (2.459)

basal area per plot, and the above environmental variables and sample factor-loading scores were described using SYSTAT version 5.0 Pearson correlation analysis (Wilkinson 1990).

RESULTS

Marsh plant associations

Marsh plant associations used in the following description of historical marsh development were derived from TWINSPAN on the 1991 matrix data. The first TWINSPAN division distinguished a wet marsh assemblage and a phreatophyte/dry marsh assemblage (Table 2). The second TWINSPAN division of the wet marsh vegetation distinguished a cattail/reed association (*Typha domingensis, Phragmites australis, Juncus* spp.) from a nonclonal herbaceous horseweed/Bermuda-grass association (*Conyza canadensis, Cynodon dactylon*). The phreatophyte/dry marsh group separated a woody perennial tamarisk/arrowweed (*Tamarix ramosissima, Pluchea sericea*) association from a dry marsh horsetail/willow (*Equisetum laevigatum* × *hyemale, Salix exigua*) association. In this paper we focused our analyses on the development and ecology of the marsh associations.

Historical marsh development

Prior to dam closure, wetland plant species were largely restricted to tributaries and off-river springs (Clover and Jotter 1944), and rematching of more than 500 pre-dam photographs confirmed this finding (Turner and Karpiscak 1980, Stephens and Shoemaker 1987, Webb et al. 1991, Webb, *in press*).

Completion of Glen Canyon Dam in 1963 resulted in development of numerous new marshes throughout the Colorado River corridor (Tables 1 and 3, Figs. 3A and 4). The earliest post-dam aerial photograph series

TABLE 3. Weighted frequency estimates of fluvial marsh area from serial aerial photographs and field inventories, 1965–1991.

Year	Source*	Patch size class categories: Very small (~0.001 ha)	Small (~0.01 ha)	Medium (~0.1 ha)	Large (~0.5 ha)	Total number	Estimated area (ha)
1965	AP	0	6	3	1	10	0.9
1973	AP/M	10	21	14	7	52	5.1
1980	AP/FI	4	30	9	6	49	4.2
1982†	FI	5	24	5	5	39	3.3
1984	AP/FI	12	4	0	1	17	0.6
1987†	FI	14	9	2	1	26	0.8
1990	AP	500	325	33	7	865	10.6
1991	FI	373	630	89	11	1103	25.0

* Source: AP, aerial photographs; M, mapping; FI, field inventory.
† Horsetail/willow marshes not inventoried.

(1965) revealed only 10 fluvial marshes with a total estimated area of 0.9 ha. No marsh vegetation was evident at the detailed study sites (Table 1). Field investigations revealed that fluvial marshes that persisted continuously since 1965 were dominated by *Phragmites* or woody phreatophytes in 1991.

In 1973 Phillips et al. (1977) documented 52 fluvial marshes with a total estimated area of 5.1 ha, from Lees Ferry to Diamond Creek. Only one of our detailed study sites (Mile 71L) showed significant development of marsh vegetation, and all return current channels (RCCs) were bare sand (Table 1).

Average marsh size increased slightly between 1973 and 1980, an increase also observed at each detailed study site (Tables 1 and 3, Fig. 4). This areal expansion occurred despite inundation of most marshes for up to 9 d by a high release of 1275 m^3/s in 1980. Marshes existed between stages associated with discharges of 425–892 m^3/s at six of the seven study sites, assuming unchanging stage-to-discharge relations from 1973 to 1991. The lack of marsh vegetation at the Mile 194L RCC was attributable to the low elevation of the bar platform, which presumably allowed recirculating flows to scour the RCC at moderate water stages. The apparent decline in marsh cover between 1973 and 1982 indicated in Table 3 was an artifact of sampling because the 1982 field inventory did not record horsetail/willow stands. Field observations indicate that little change in marsh distribution took place between 1980 and 1982.

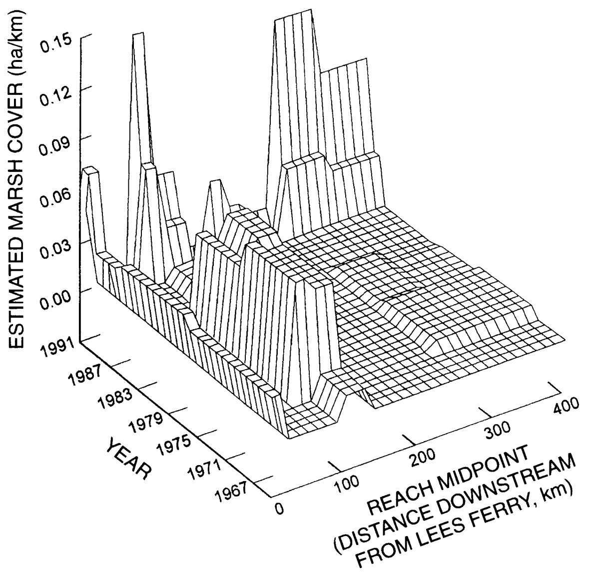

FIG. 4. Changes in estimated cover of fluvial marsh area (ha/km) between 1965 and 1991 in the 11 geomorphic reaches of the post-dam Colorado River, Grand Canyon National Park, Arizona. Marshes developed after scouring flows in 1965, particularly in wide reaches (Table 4). Marshes scoured by high flows in 1983–1986 quickly redeveloped between 1987 and 1991. Marsh colonization accelerated after 1986 flooding as compared to the period from 1965 to 1983.

Flooding in 1983 scoured more than 85% of the marshes from the river corridor, including 42% of the *Phragmites* and 93% of the *Typha* marshes (Stevens and Waring 1985), leaving 17 marshes and a total area of 0.6 ha. All study sites were scoured in 1983, eliminating all above- and most below-ground growth of wetland plant species. Recolonization was prevented by high flows from 1984 to 1986 (Tables 1 and 3, Fig. 4).

In 1987, we observed 26 cattail/reed marshes (Tables 1 and 3) that occupied a total area of 0.8 ha between Lees Ferry and Diamond Creek. Recolonization of RCCs began in 1987 following aggradation of $\geq$0.2 m of tributary-derived, river-deposited silty fine sand at all detailed study sites. Wet marsh taxa had colonized all study sites by late 1987, and *Typha* and *Phragmites* became dominant at miles 43L, 55.5R, 71L, and 194L by 1989. Between 1987 and 1990 marsh vegetation colonized down to stage elevations that were inundated 30% of the days.

June 1990 aerial photographs revealed 865 marshes with a combined area of at least 10.6 ha of fluvial marsh habitat. Rapid expansion of small marshes occurred between June 1990 and October 1991.

In October 1991, there were 730 marshes between Lees Ferry and Diamond Creek, excluding very small marshes (Tables 3 and 4). The marsh area in the Grand

TABLE 4. Geomorphic characteristics and 1991 fluvial marsh inventory in 11 reaches of the Colorado River between Lees Ferry and Diamond Creek, Grand Canyon National Park, Arizona, excluding 31 marshes associated with springs or tributaries. Reach descriptions follow Schmidt and Graf (1990). One SD for mean area data is included parenthetically.

Reach	Reach length (km)	Mean reach width (m)*	Marsh density (no./km) Wet marsh	Marsh density (no./km) Dry marsh	Marsh density (no./km) Total	Mean marsh area (ha) Wet marsh	Mean marsh area (ha) Dry marsh	Mean marsh area (ha) Total	Total marsh area (ha)	Marsh cover (ha/km) Wet marsh	Marsh cover (ha/km) Dry marsh	Marsh cover (ha/km) Total
Permian Reach	17.7	85.3 W	.51	.11	.62	.10 (.120)	.03 (.24)	.09 (.108)	.77	.04	<.01	.04
Supai Gorge	18.5	64.0 N	.22	.11	.32	<0.1 (.010)	<.01 (.005)	<.01 (.008)	.31	<.01	<.01	<.01
Redwall Gorge	28.0	67.1 N	.07	.25	.32	.01 (.015)	.01 (.007)	.01 (.009)	.74	<.01	<.01	<.01
Lower Marble Canyon	34.6	106.7 W	1.88	1.91	3.85	.05 (.118)	.03 (.082)	.04 (.101)	5.14	.08	.06	.15
Furnace Flats	25.4	118.9 W	1.18	1.50	2.68	.04 (.060)	.01 (.012)	.02 (.042)	1.46	.04	.02	.06
Upper Granite Gorge	64.8	57.9 N	.05	.96	1.00	.02 (.018)	.01 (.008)	.01 (.009)	.49	<.01	<.01	.01
Aisles Reach	12.2	70.1 N	.16	2.78	2.94	.02 (.014)	.02 (.016)	.02 (.016)	.64	<.01	.05	.05
Middle Granite Gorge	23.0	64.0 N	.04	1.43	1.57	.08 (···)	.02 (.024)	.02 (.026)	.45	<.01	.02	.02
Muav Gorge	32.0	54.9 N	.19	.72	.91	.01 (.015)	.01 (.021)	.01 (.019)	.40	<.01	.01	.01
Lower Canyon Reach	86.6	94.5 W	1.34	5.11	6.47	.03 (.034)	.02 (.045)	.02 (.043)	12.58	.04	.11	.16
Lower Granite Gorge	18.7	73.2 N	.75	7.23	8.04	.04 (.046)	.01 (.015)	.01 (.022)	1.98	.03	.08	.11
Totals or grand means	362.8	79.0	.70	2.33	3.04	.04 (.071)	.02 (.041)	.02 (.050)	24.96	.02	.04	.07

* Schmidt and Graf (1990): N = narrow reach; W = wide reach.

Canyon (24.6 ha) had more than doubled since June 1990. An additional 373 very small marshes (mostly horsetail/willow) contributed 0.40 ha (1.6%), for a total marsh cover of 25.0 ha. This total included 253 (22.9%) wet marshes comprising 9.0 ha (36%), and 850 horsetail/willow marshes. Overall, marshes comprised approximately 1% of the riparian habitat between Lees Ferry and Diamond Creek in 1991. Although fewer in number, cattail/reed marshes were larger (mean area = 0.04, 1 SD = 0.071 ha) than horsetail/willow marshes (0.02, 1 SD = 0.041; ANOVA $F_{1,\ 1088} = 26.169$, $P < 0.001$). In 1991, small wet marshes occupied three of the seven detailed study sites (miles 43L, 123L, and 172L) and moderate to large wet marshes occupied the other sites (miles 51L, 55.5R, 71L, and 194L; Table 1).

Excluding very small marshes, the mean establishment rate of wet marshes from 1986 to 1991 was 32.0 marshes/yr, sixfold higher than the 1965 to 1973 rate of 5.3 marshes/yr documented by Phillips et al. (1977).

Spatial scale patterns

System-wide scale.—Colorado River marsh density (number per kilometre) was positively correlated with distance from Glen Canyon Dam ($R^2 = 0.847$, $F_{1,\ 9} = 22.221$, $P = 0.001$; Table 4) in 1991. In particular, horsetail/willow patch density increased with distance downstream. Marsh cover (hectare per kilometre of river) increased with distance downstream ($F_{1,8} = 12.522$, $P = 0.008$; Table 4); however, mean individual marsh area decreased with distance. This was attributable to the high density of small, dry marshes in the Lower Canyon reach (Mile 160 to Mile 214).

Reach (intermediate) scale.—Marsh density per kilometre was greater in wide geomorphic reaches than in narrow reaches ($\chi^2 = 3596.8$, df = 10, $P < 0.001$), and mean marsh area was also greater in wide reaches (univariate $F_{1,\ 9} = 9.836$, $P = 0.012$; Table 4, Fig. 4). Marsh density and cover were positively correlated with channel width in the different reaches (density $R^2 = 0.716$, univariate $F_{1,\ 9} = 26.168$, $P = 0.001$; cover $R^2 = 0.533$, univariate $F_{1,\ 9} = 12.436$, $P = 0.06$). Wet and dry marshes were restricted to wide reaches upstream from Mile 125, but were smaller, more numerous, and occurred in all reaches downstream from Mile 125 (Table 4).

Local scale.—Marshes occurred in low-lying, fine-grained geomorphic settings within individual eddies (e.g., reattachment bar and upper pool RCCs, and bar platforms) and on channel margins deposits, but rarely on low-lying, cobble/boulder debris fans. Comparison of marsh distribution among the various deposit types with the total number of various deposit types in the system revealed that fluvial marshes occurred disproportionately more often on channel margin and separation deposits (especially *Phragmites* and horsetail/willow stands in the lower Grand Canyon) and disproportionately less often on reattachment deposits, par-

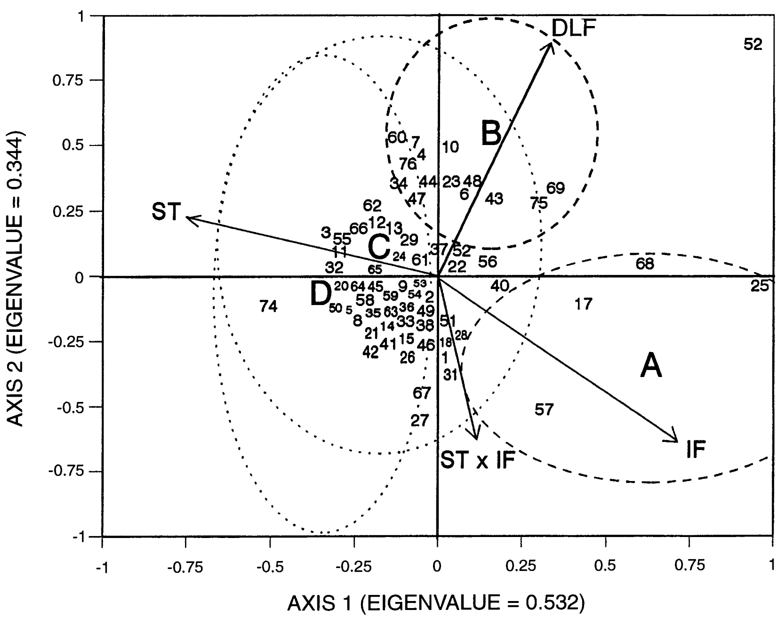

FIG. 5. Species factor loading scores in samples space for the first two CCA axes. Species scores were derived from ordination of the matrix of 307 1.0-m^2 plots and 76 marsh plant species from seven Colorado River marshes in the Grand Canyon. Numbers refer to species listed in Table 2. Letters refer to the four TWINSPAN vegetation associations: wet marsh (A) cattail/reed (*Typha domingensis*/*Phragmites australis*), and (B) horseweed/Bermuda-grass (*Conyza canadensis*/*Cynodon dactylon*); (C) woody phreatophyte tamarisk/ arrowweed (*Tamarix ramosissima*/*Pluchea sericea*); and (D) dry marsh horsetail/ willow (*Equisetum laevigatum* × *hyemale*/*Salix exigua*). Ellipses represent 1 SD around the mean species factor loading score centroid for each association. Arrows indicate the relative importance and direction of environmental variables: IF, daily inundation frequency; ST, soil texture; ST × IF, interaction term between soil texture and daily inundation frequency; and DLF, distance from Lees Ferry, in kilometres.

ticularly in the upper reaches ($\chi^2 = 48.341$, df = 3, $P < 0.001$).

Microsite scale.—Daily inundation frequency, soil texture, and distance from Glen Canyon Dam strongly influenced the distribution of marsh taxa (Fig. 5). The first three CCA axes explained 94% of the species-to-environment interaction. Axis 1 (eigenvalue = 0.521) accounted for 44.4% of the species-to-environment relationship. Pearson correlation analysis indicated that axis 1 was negatively correlated with soil texture (Bonferroni-adjusted $P < 0.001$) and positively correlated with daily inundation frequency and distance downstream ($P < 0.001$ for both; Table 5). Soil texture and daily inundation frequency were negatively correlated ($P < 0.001$) because silt and clay fractions were deposited during lowest stages when velocity was reduced. More than 95% of the cattail/reed cover occurred between the 300 and 700 m^3/s stage elevations at the detailed study sites (Fig. 6), and cover of this association increased to some extent with distance downstream. Eighty percent of wet marsh cover occurred below the 566 m^3/s stage, which was inundated 50% of the days from 1986 through 1991 as marshes rapidly redeveloped after 1983–1986 flooding.

The effects of soil texture and inundation frequency on marsh composition was further elucidated by CCA axes 2 and 3 (Fig. 5). CCA axis 2 (eigenvalue = 0.344) explained an additional 29.3% of the species-to-environment relationship, and was strongly positively correlated with inundation frequency and distance, and negatively correlated with interaction between inundation frequency and soil texture ($P < 0.001$ for all three factors; Table 5). Interaction effects were due to the nonlinear response of marsh plants to daily inundation frequency: no marsh plant species persisted in habitats that were permanently inundated or inundated on a daily basis, regardless of soil texture. The negative correlation with distance was attributable to the decrease in inundation frequency as the range of daily flows attenuates with distance downstream from the dam.

CCA axis 3 was negatively correlated with soil texture ($P < 0.001$), and positively correlated with distance ($P = 0.02$) and interaction between inundation frequency and soil texture ($P < 0.001$; Table 5). Axis 3 (eigenvalue = 0.238) explained an additional 20.1% of the species-to-environment relationship. Cattail/reed stands occupied silty loam soils that were finer in texture than the loamy sand soils occupied by horseweed/ Bermuda-grass stands or the sand soils occupied by tamarisk/arrowweed and horsetail/willow stands ($F_{3,303} = 33.34$, $P < 0.001$; post hoc Tukey $P < 0.001$; Table 2). Data from all detailed study sites corroborated this finding. For example, 98% of the cattail/reed vegetation at the Mile 194L marsh occurred on silty loam soils, rather than on the fine/medium sand soils that domi-

TABLE 5. Pearson correlation analysis describing correlation between environmental variables, sample scores of 4 CCA axes from 307 1.0-m^2 plots in seven Colorado River marshes in the Grand Canyon, and covarying biotic parameters. Environmental variables include daily inundation frequency (IF), surficial soil texture (ST), interactions between these variables, and distance from Lees Ferry, Arizona (DLF, in kilometres). Daily inundation frequency is grouped into 10 categories in increments of 0.1. Soil texture classes include: 1 = clay, 2 = silt/clay, 3 = silt, 4 = silty fine sand, 5 = fine sand, 6 = medium sand. Covarying biotic variables include: total plot basal area per square metre (TBA) and species density (*S*, no./m^2). Bonferroni-adjusted *P* values are included. As a function of the CANOCO program, axis factor loading scores are not correlated (P = 1.000 in all pairwise comparisons) and are not shown.

	Environmental variables			Covarying biotic variables	
	IF	ST	DLF	*S*	TBA
IF	1.000				
P	0.000				
ST	−0.453	1.000			
P	0.000	0.000			
DLF	−0.204	−0.140	1.000		
P	0.011	0.512	0.000		
S	0.118	−0.236	−0.063	1.000	
P	1.000	0.001	1.000	0.000	
TBA	0.120	−0.123	0.059	−0.108	1.000
P	1.000	1.000	1.000	1.000	0.000
Axis1	0.588	−0.613	0.332	0.003	0.269
P	0.000	0.000	0.000	1.000	0.000
Axis2	−0.447	0.133	0.665	−0.212	0.036
P	0.000	0.711	0.000	0.007	1.000
Axis3	−0.076	−0.207	0.180	0.295	−0.254
P	1.000	0.009	0.057	0.000	0.000
Axis4	−0.093	0.226	0.019	−0.060	−0.044
P	1.000	0.002	1.000	1.000	1.000

nated the reattachment bar platform. The positive correlation with distance reflects a cumulative increase in fine sediments through the river corridor: the depth of silty fine sand ranged from 0.2 m in the Mile 43 RCC to >1.5 m at Mile 194L RCC.

In summary, daily inundation frequency and soil texture interactively affected the distribution of marsh vegetation at the microsite scale (Tables 2 and 5; Fig. 5). The wet marsh cattail/reed association occupied silty loam soils that were inundated, on average, 54% of the days (Fig. 7A). The wet marsh horseweed/Bermuda-grass association was dominated by disturbance-tolerant taxa, and occupied higher velocity (more highly disturbed) RCC mouths and channel margins (Fig. 7B). The tamarisk/arrowweed and dry marsh horsetail/willow associations occupied drier, coarser, less disturbed sandy soils around marsh peripheries, on bar platforms, and along channel margins, with mean daily inundation frequency of 16 and 18%, respectively (Fig. 7C and 7D, respectively). Therefore, conditions that promoted development of the cattail/reed association contrasted strongly with those that promoted development of woody phreatophyte stands.

Marsh standing mass

Standing ash-free dry mass (AFDM) varied in relation to association type, inundation regime, and soil

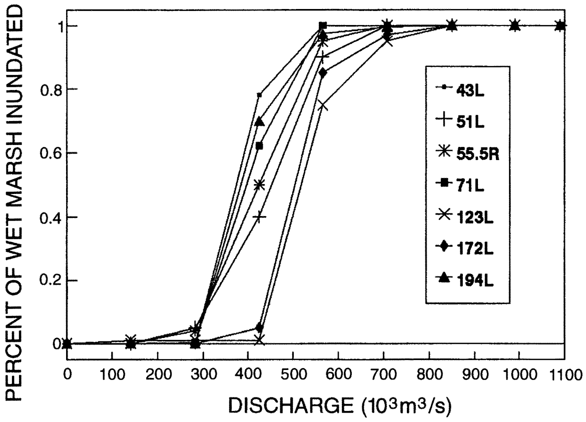

FIG. 6. Daily inundation frequency of wet marsh associations at seven fluvial marsh sites in the Colorado River corridor, Grand Canyon. Wet marsh vegetation occupied sites lying within the range of normal dam operations, while dry marsh vegetation (not shown) occurred across a broader range of inundation frequencies.

texture. Mean AFDM in mainstream marshes was 641 g C/m^2 (n = 28, 1 SD = 579.7 g C/m^2) in 1991, with more than 90% as living plant tissue (Table 1). Maximum AFDM occurred in RCCs covered by *Typha* (e.g., Mile 194L), while the lowest AFDM occurred in bar platform marshes dominated by low-growing annual or nonclonal herbs (e.g., Mile 55.5R), or in higher, less frequently inundated RCCs (e.g., Mile 123L). We observed little litter in marsh understories and plant photosynthetic surfaces were often coated with silt from fluctuating flows.

Mean total basal area (TBA, cm^2/m^2) likewise differed between vegetation associations (univariate $F_{1,305}$ = 11.045, P = 0.001; Fig. 7). The grand mean TBA in 1991 was 27.3 cm^2/m^2 (n = 307, 1 SD = 55.935 cm^2/m^2). TBA was greater in cattail/reed and tamarisk/arrowweed stands than in horseweed/Bermuda-grass or horsetail/willow stands (post hoc Tukey $F_{3,303}$ = 7.689, P < 0.001; Table 2). TBA was nonlinearly correlated with daily inundation frequency. Highest TBA (72.9 cm^2/m^2, n = 15, 1 SD = 110.712 cm^2/m^2) occurred on plots that were inundated 65% of the days, and TBA decreased at higher and lower inundation frequencies. TBA was not correlated with soil texture, but trended towards maximum values on clay/silt loam soils (Table 5, Fig. 7).

Marsh diversity

Species density (*S*, number per square metre) on belt transect plots varied between associations and environmental variables (Tables 2 and 5). Grand mean *S* among these 5-yr-old marshes was 4.7 species/m^2 (n = 307, 1 SD = 2.51 species/m^2). The horseweed/Bermuda-grass association was dominated by low-growing annual herb taxa, and supported a wide variety of rare taxa that were more closely associated with other assemblages. Mean *S* was highest (5.8 species/m^2, n =

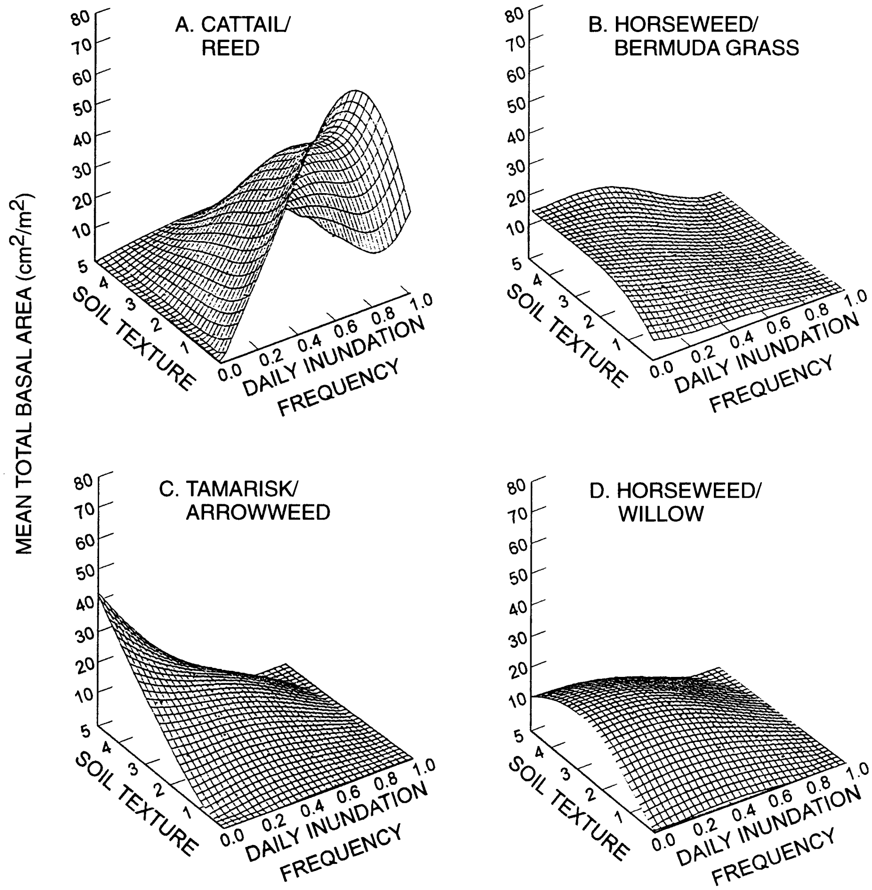

FIG. 7. Mean total marsh vegetation basal area (cm^2/m^2) in response to inundation frequency and soil texture classes (see Table 5) on 307 1.0-m^2 plots from seven Colorado River marshes: (A) wet marsh cattail/reed, (B) wet marsh horseweed/ Bermuda-grass, (C) woody phreatophyte tamarisk/arrowweed, and D) dry marsh horsetail/willow associations.

18, 1 SD = 2.02 species/m^2) on plots with silt loam soils and S decreased in coarser soil textures (Table 5). Mean S was highest (7.0 species/m^2, n = 13, 1 SD = 2.55 species/m^2) on plots inundated 60% of the days, and decreased at both lower and higher daily inundation frequencies.

Fluvial marshes along unregulated tributaries

Unregulated tributary streams supported more, but smaller and compositionally different, fluvial marshes than did the regulated mainstream. Tributary marshes consisted of strandline monocultures of *Phragmites, Typha, Cladium californicum,* or *Scirpus pungens,* but typically lacked *Equisetum laevigatum* × *hyemale* and low-growing herbs (e.g., *Gnaphalium chilense* and *Plantago* spp.), which characterized mainstream marshes. Pooled mean density of tributary marshes was 9.4 marshes/km of channel (n = 12, 1 SD = 11.754 marshes/km), threefold greater than mainstream marsh density. Mean tributary marsh area was 0.01 ha/marsh (n = 105 marshes in a total of 14.5 km inventoried, 1 SD = 0.016 ha/marsh), one-third the mean area of mainstream marshes. Tributaries in which no marshes were found (e.g., Havasu Creek) had sustained recent flooding.

DISCUSSION AND CONCLUSIONS

River regulation and fluvial marsh development

Flow regulation of the eddy-dominated Colorado River downstream from Glen Canyon Dam provides an unanticipated ecosystem experiment demonstrating strong linkage among geomorphology, flow regulation, and fluvial marsh development and structure. Colorado River marshes, which were previously restricted to springs and perennial tributaries, dramatically increased in number and size after reduction of flood frequency. Fluvial marshes formed from 1965 to 1982 under regulated daily varial flows that were <2.5 times the grand mean discharge (325 m^3/s). Marshes persisted through small regulated floods of up to 1275 m^3/s, but were scoured in 1983 when discharge exceeded 1700 m^3/s. The 1983 flood was fivefold higher than the post-dam mean annual flow and equivalent to a normal pre-dam annual peak flow. High flows from 1983 to 1986 prevented reestablishment of marsh taxa. Marsh establishment rate increased more rapidly between 1987 and 1991 (32.0 wet marshes/yr) than from 1965 and 1973 (5.3 marshes/yr), probably because of greater propagule abundance in the latter period. Thus, the initial post-dam colonization by marsh vegetation ensured subsequent resiliency after high scouring flows.

The resiliency of Grand Canyon marshes under flow regulation stands in marked contrast to wetland losses in the highly regulated, largely alluvial lower Colorado River downstream from Hoover Dam (Ohmart et al. 1988). Flood control there since 1935 has prevented regeneration of shallow backwater habitats in which marshes develop. Progressive aggradation of backwaters and encroachment of non-native phreatophytes has essentially eliminated the natural fluvial marshes that existed there prior to flow regulation.

Wetland and riparian vegetation development is strongly influenced by both dam-induced flood control and daily flow conditions. Large daily flow fluctuations increase the wetted area of river banks, and therefore increase the bar area available for colonization. However, flow fluctuations can exacerbate erosion (Schmidt and Graf 1990, Beus and Avery 1992), thereby limiting the bar area available for marsh development. Daily fluctuations flatten marsh vegetation, export litter, and coat photosynthetic surfaces with silt, particularly during periods of tributary inflow. Although not examined here, hypolimnetic dam discharge results in cold water temperatures that may limit marsh productivity, decomposition rates, and anaerobiosis. Ice damage, which strongly affects boreal marsh vegetation (e.g., Day et al. 1988), exerted little impact on this desert-regulated river ecosystem.

Spatial scale and marsh development

Fluvial marsh distribution varies in relation to the spatial scale of inquiry, especially in large rivers in complex landscapes. System-wide scale effects of geologic structure, reach scale effects of bedrock characteristics and tributary impacts, and local scale geomorphic setting largely control the distribution of silty fine sand deposits (silty loam soils), which are required for ecesis of marsh taxa. Stage elevation controls inundation frequency, soil moisture and, in many regulated rivers, sheer stress, thereby affecting microsite conditions and assemblage composition. Overall, our results indicated that reduction of flood frequency by flow regulation increased the relative importance of geomorphic setting on the development of riparian wetland vegetation.

Cumulative input of tributary-derived silt and marsh propagules over distance should result in greater abundance of fine-grained deposits and greater probability of marsh plant establishment, thereby increasing overall marsh area downstream. Although Colorado River marsh density was positively correlated with distance downstream, marsh size was negatively correlated with distance. Flow attenuation decreases the wetted bar area available for marsh occupation, and sand bar instability increases with distance downstream (Beus and Avery 1992), thereby limiting marsh size.

At reach and local spatial scales, channel constrictions and eddies are relatively rare in alluvial rivers, where channels meander and transitory bar and bank features exert dominant influences on floodplain vegetation (e.g., Johnson et al. 1976, Kalliola and Puhakka 1988, Kalliola et al. 1991). In contrast, channel constrictions are numerous in the eddy-dominated Colorado River, and marshes there develop in the low velocity depositional environments associated with these constrictions.

In contrast to larger spatial scales, microsite inundation frequency and soil texture influence marsh associations similarly in both eddy-dominated and alluvial rivers (Auclair et al. 1976, Day et al. 1988). This is not surprising because water table depth, soil texture, and other microsite characteristics directly influence plant establishment and growth (Grubb 1977, van der Valk 1981). Colorado River regulation increased microsite stability by reducing seasonal flow-related disturbance within discrete stage elevation zones. Thus, flow regulation increased the relative importance of geomorphology at several spatial scales and permitted marsh development in this system.

Fluvial marsh standing mass

Marsh standing mass (SM) appears comparable between eddy-dominated and alluvial rivers, and between regulated and uncontrolled rivers. Average Colorado River marsh AFDM (640 g C/m^2) was comparable with values reported for alluvial river marshes. For example, unashed SM along the alluvial Ottawa River ranged from 30 to 1100 g C/m^2 (Day et al. 1988), and averaged 845 g C/m^2 in Huntingdon Marsh on Lake St. Francis (Auclair et al. 1976), which sustained lower flow velocities and little daily fluctuation as compared to the Colorado River. Gorham (1974) reported that sedge marsh SM varied between 700 and 1400 g C/m^2 across a moisture gradient in warm climates, again comparable with our Grand Canyon data.

Litter retention is limited in alluvial and eddy-dominated river marshes, and in regulated and unregulated river marshes. Auclair et al. (1976) reported that two-thirds of the annual production in Huntingdon Marsh was exported annually by water level regulation, leaving 281 g $C \cdot m^{-2} \cdot yr^{-1}$. Colorado River marshes contained little leaf litter or duff, indicating that litter was exported from marshes under daily fluctuating flows rather than being incorporated into marsh soils. Although the mainstream marshes we examined were only 5 yr old in 1991, other riparian habitats scoured by 1983–1986 flows but lying above the fluctuating flow zone, showed substantial litter accumulation. Fluctuating flows also flattened marsh vegetation and coated photosynthethic surfaces with silt, probably reducing production.

Litter retention appeared equally low in unregulated tributary marshes and regulated mainstream marshes. In contrast, we observed substantial litter retention in spring-fed marshes that had not been disturbed by flooding, further indicating that fluvial marsh litter accumulation was limited by scouring flows. Thus, both unregulated and regulated river marshes lose organic production to inundating flows. The magnitude of litter export from regulated vs. unregulated fluvial marshes deserves further study.

Fluvial marshes and flow management

Effective management of regulated fluvial wetlands requires understanding existing and potential marsh distribution, associated wildlife habitat relationships, and marsh responses to flow patterns, all in the context of clearly defined management goals and objectives (Risser and Harris 1989). Our data demonstrate that flow regulation of the Colorado River by Glen Canyon Dam permitted widespread development of productive and diverse fluvial marshes, which were formerly rare. Assuming that 1991 patterns of low marsh stability, high marsh resilience, and soil texture distribution persist in this system, we predict that reduction of daily inundation frequency will result in increased wet marsh colonization at lower stage elevations and gradual transition of existing cattail/reed marshes to woody phreatophyte vegetation at higher stage elevations (Fig. 7). Reduced inundation frequency should accelerate aggradation of low-lying bar surfaces, also driving composition towards dominance by woody phreatophytes. In contrast, increased mean discharge and daily inundation frequency should eliminate low-lying vegetation, coarsen soil texture, and restrict marshes to higher stage elevations.

Marshes in regulated, constrained rivers exhibit limited stability under erratic high releases, but if tributary-derived fine sediment deposits remain available, marshes may become increasingly resilient. Although the resiliency of marsh vegetation may increase following regulation, obligate wetland fauna may not share that resiliency. Wildlife populations that require marsh habitat may not persist through a several-year hiatus in habitat availability following unplanned flooding events or other inconsistent management practices.

Proliferation of wetland vegetation downstream from dams may be considered, to some extent, as mitigation for upstream habitat losses (Risser and Harris 1989). In light of potential local and regional increases in productivity, diversity, and habitat availability, river managers are faced with important questions: Should regulated rivers be managed for marsh development? If so, what marsh distribution, composition, and level of productivity is appropriate? To what extent and at what cost should flow regimes that cause expansion of wetlands be implemented? What are the trade-offs between wetland and riparian vegetation, fisheries or wildlife habitat, recreation and other resource conditions? Should planned flooding be used to restore low-lying geomorphic habitats on which marshes develop, and if so, at what frequency, magnitude, and cost to other resources? The authors of this article disagree among themselves on the answers to these management questions. It may be inappropriate to sacrifice natural ecological components (e.g., open sand bars in the Grand Canyon) to increase diverse and regionally significant naturalized habitats, such as fluvial marshes. However, the strong linkage between river regulation and wetland vegetation development demands that such questions be asked and answered in the context of clearly defined river management goals.

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